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RESEARCH ARTICLE

Effects of environmental factors and predation on benthic communities in headwater streams

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Abstract Structure and composition of benthic macroinvertebrate assemblages were investigated during three consecutive years in six headwater streams that exhibit a high variation in environmental conditions, habitat structure and predatory pressure. We examined whether the abundance of functional feeding groups could be best predicted by the abundance of predators and some habitat and chemical variables. Mean density and biomass of macroinvertebrate functional feeding groups varied significantly throughout the study area. Stepwise multiple regression analyses revealed that both density and biomass of functional feeding groups was influenced primarily by chemical features of water. Shredder biomass and scraper density were also influenced by habitat features, the abundance of scrapers increasing in deeper localities at lower altitudes and with abundant macrophytes. The abundance of predatory invertebrates was related to the density and biomass of benthic prey. An influence of fish predation on invertebrate communities was not observed in the study streams. The finding that benthic communities in undisturbed headwater streams are mainly affected by water chemistry variables irrespective of fish predation and habitat features clearly highlight the sensitivity of functional feeding groups to changes in chemical features and their role as indicators for bioassessment.

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Introduction

Several studies have suggested that headwaters are vital for preserving the health of whole river networks and as important habitats for maintaining biodiversity (Clarke et al. 2008). While many taxa contribute to biodiversity in headwater streams, macroinvertebrates play a central ecological role in many systems, and are among the most ubiquitous and diverse group of organisms (Strayer 2006). Human disturbances such as riparian clearing, nutrient enrichment or introduction of exotic species, can change macroinvertebrate communities, thus modifying food web structure. Therefore, the use of benthic macroinvertebrates as indicators of river health is becoming legislated and mandatory in Europe with the introduction of the water framework directive (WFD) (Directive 2000/60/CE, 2000). Assessment of river health within the WFD relies upon a comparison with the status in undisturbed reference conditions, mostly restricted to headwaters in the Mediterranean region.

Benthic macroinvertebrates are supposed to be sensitive to both physical and chemical disturbances (Furse et al. 2006). However, some controversy exists concerning the usefulness of biotic indexes for the assessment and classification of ecological quality status, especially when the knowledge of the ecosystem of interest is scarce (Díaz et al. 2004). Thus, the implementation of the WFD implies a clear knowledge of the factors that most influence the structure of macroinvertebrate communities in conditions of minimal anthropogenic impact. Further, knowledge gaps concerning the ecological preferences are a major obstacle in analysing the impact of climate change and other emerging stressors, especially in the highly variable Mediterranean (Hering et al. 2009). Therefore, a good understanding of the relative roles of predators, habitat and water chemistry in structuring macroinvertebrate communities in headwaters seems essential.

The abundance of stream invertebrates is known to be influenced by hydraulic conditions (Monk et al. 2008), substratum composition (Downes et al. 2000), temperature (Haidekker and Hering 2008) and water chemistry, so that density typically increases with nutrient enrichment (e.g. Cross et al. 2006; Gafner and Robinson 2007). The importance of substratum to macroinvertebrate communities has been recognized for a long time. Substratum surface provide attachment sites and shelter from predators, and permit the development of an epilithic layer, which serves as food for many species, especially scrapers (Downes et al. 2000). In headwater streams, leaf packs may also provide benthic invertebrates with a refuge from fish predation (Ruetz et al. 2006).

On the other hand, food resources also influence macroinvertebrate communities in headwaters. Thus, resource supply for many stream invertebrates originates directly from primary production, but also can be supported by allochthonous inputs (Polis et al. 1997; Jefferies 2000; Álvarez and Pardo 2009). Further, the input of detrital materials from the riparian vegetation to streams, mostly leaf litter, has long been recognized as a critical contribution to the functioning of upland wooded streams (Wallace et al. 1997; Clarke et al. 2008). However, the riparian forest may limit primary production due to its shading effect and therefore food availability for herbivores and their subsequent abundance (Wallace et al. 1999).

Finally, some studies have found that fish can substantially alter invertebrate communities through direct and indirect trophic effects (e.g. Biggs et al. 2000; De Lange et al. 2004; Blanchet et al. 2008). However, there is little consensus about the effects of predatory fish on invertebrate abundance (Cooper et al. 1990; Power 1992). An effect of predatory fish on benthic prey may be augmented by predatory invertebrates, which can considerably reduce benthic populations (Blumenshine and Hambright 2003; Bengtson et al. 2008). Some studies have investigated the simultaneous influence of predators and resource supply on the dynamics of macroinvertebrate communities. For detritus-based stream food webs, previous results support a role for both predators and resources in controlling the structure of the invertebrate communities (e.g. Nyström et al. 2003; McIntosh et al. 2005).

The main objective of this study was to identify the factors that most influence the structure of macroinvertebrate communities in six headwater streams that exhibit a high variation in environmental variables, habitat structure and predatory pressure. In particular, we examined whether the spatial variation in abundance of functional feeding groups could be best predicted by the abundance of predators and some habitat and chemical variables.

Materials and methods

Study area

This study was carried out in 15 localities from six Spanish streams; four are tributaries to the River Tajo (Cabrillas, Gallo, Dulce, Jarama) and two to the River Duero (Cega, Eresma). The streams were selected on the basis that they encompass a wide range of environmental conditions within a limited area. The study reaches correspond to first-order streams and range from 39°50′N to 41°42′N latitude and from 2°03′W to 4°45′W longitude. The streams are relatively unaffected by land use or pollution. The streams Jarama, Cega and Eresma arise from granite and gneiss catchments at elevations between 1,100 and 1,300 m. The greater part of their water comes from surface drainage and they become torrential in their upper reaches at snowmelt in spring. The other streams run through limestone bedrock at elevations from 850 to 1,400 m. The geology of the latter basins and the mild climate gives an even flow regime throughout the year. Riparian vegetation at Cabrillas, Gallo, Dulce and Jarama is dense and mainly comprises a deciduous forest with *Populus nigra* L., *Salix* spp., *Fraxinus angustifolia* Vahl, *Quercus pyrenaica* Willd., *Betula pendula* Roth, *Frangula alnus* Miller and *Crataegus monogyna* Jacq. as the main species. In Cega and Eresma, the channel is surrounded by a well-developed riparian forest dominated by *Pinus sylvestris* L., although deciduous species such as *Salix* spp. and *F. alnus* are also present. Further details of the study area are given in Almodóvar et al. (2006).

Benthic macroinvertebrates

Benthic macroinvertebrates were sampled in each locality every March, June, September and December from March 1996 to December 1998. Three to four replicate samples per site, taken progressively upstream of each other, were collected on each sampling date with a cylinder core-type sampler (Edmondson and Winberg 1971) (55-cm height, 35-cm diameter and 250-µm mesh size). Samples came from different mesohabitats to cover the existing environmental variability. Invertebrate samples were preserved in 10% formalin for later laboratory identification, sorting and counting. Specimens were dried in an oven at 60°C for 24 h and density and biomass (dry weight to the nearest

0.001 g) were calculated. All specimens were identified to the lowest possible taxonomic level using the available taxonomic keys (i.e. species when possible, otherwise usually genus). Each taxonomic group was assigned to one of five functional feeding groups: predators, scrapers, shredders, collector-filterers and collector-gatherers, according to Merritt and Cummins (1996) and Tachet et al. (2000).

Fish community

Fish were sampled every March, June, September and December from March 1996 to December 1998 at each site by electrofishing using a 2200 W DC generator. Fish were anaesthetised with tricaine methane-sulphonate (MS-222) and their fork lengths (to the nearest mm) and masses (to the nearest g) were measured. Scales were used for age determination. The fish were placed in holding boxes to recover and then returned to the stream. Fish densities (fish ha^{-1}) with variance were estimated separately for each sampling point by the maximum likelihood method (Zippin 1956) and the corresponding solution proposed by Seber (1982) for three-removals assuming constant-capture effort.

Environmental variables

Each time a biological sample was taken field measurements of water and habitat were recorded. Habitat variables were estimated at each locality following Platts et al. (1983). Transects were spaced 10 m apart and point measurements were made along the transects at 1 m intervals. At each point, water column depth (cm) and current velocity (m s^{-1}) were measured. In further analyses, the annual coefficient of variation of current velocity was used. The proportion of substratum, submerged vegetation and canopy cover were visually estimated to the nearest 5% in each 1 m^2 quadrat within each transect. The substratum class within each quadrat was classified according to Platts et al. (1983) as silt (particle size <0.6 mm), sand (0.6–5.0 mm), gravel (5.0–76.0 mm), cobble (76.0–305.0 mm), boulder (more than 305.0 mm) and bedrock. A mean substratum index was calculated for each quadrat according to Baltz et al. (1991) by coding classes in order of coarseness: 1 = silt; 2 = sand; 3 = gravel; 4 = cobble; 5 = boulder; 6 = bedrock; then multiplying each proportion as follows:

$$\text{Substratum index} = [(1\%_{\text{Silt}}) + (2\%_{\text{Sand}}) + (3\%_{\text{Gravel}}) + (4\%_{\text{Cobble}}) + (5\%_{\text{Boulder}}) + (6\%_{\text{Bedrock}})]/100$$

At each site, transects were set parallel to the stream channel to assess riparian vegetation structure, species composition and cover. Three transects of 1 m width and 100 m length were set randomly on each side of the stream near the bankfull boundaries of the channel. All trees, shrubs and herbs were identified to species and percentage cover was estimated to the nearest 5%. We classified species as either deciduous or non-deciduous to estimate the mean cover of deciduous vegetation in the riparian forest. The percentages corresponding to trees (0–100%), shrubs (0–100%) and herbs (0–100%) were added and used in further analyses as a surrogate measure of the allochthonous input of organic matter into the streams.

Water samples were taken seasonally from each sampling site from 1996 to 1998 to determine conductivity, total dissolved solids, pH, chloride, sulfate, phosphate, alkalinity, nitrate, nitrite, sodium, potassium, calcium, magnesium and ammonia. Conductivity and TDS were measured in situ with a Hach Model 44600 portable conductivity/TDS meter (Hach Company, Loveland, Colorado) and pH with a Hach Model 43800 portable pH meter (Hach Company, Loveland, Colorado). Alkalinity was determined by means of the sequential titration procedure with a Hach Model 16900 Digital Titrator. Nutrient concentrations were determined by a series of chemical reactions with a Hach Model 45250 DR/2000 Spectrophotometer (Hach Company, Loveland, Colorado). The ions Na^+, K^+, Ca^{2+} and Mg^{2+} were estimated by atomic-absorption spectroscopy. The water temperature was measured by means of data-loggers (Vemco, Halifax, Nova Scotia, Canada) permanently placed in each river during the study period.

Statistical analyses

Differences in water quality and habitat variables between localities were explored by means of principal components analysis (PCA), with a correlation matrix, because of the large number of variables and the fact that some were correlated. The data were standardized before the analyses were done. The between-localities PCAs reduced the number of explanatory variables by defining independent synthetic variables (linear combinations of chemical water and habitat characteristics) that best reflected between-localities variations in water quality patterns and habitat features.

Fish and macroinvertebrate abundance were analysed according to hierarchical designs. Nested repeated-measures ANOVAs were used to assess the effects of space (sampling sites nested within rivers) and time (repeated measures at sequential sampling times) on density and biomass of functional feeding groups, as well as on fish density.

Correspondence analysis (CA) was used as a visualization tool to evaluate the macroinvertebrates assemblage structure in each sampling locality. The effect of environmental variables and predation on abundance of functional feeding groups was tested using multiple regression analyses. Forward stepwise multiple regression analyses were performed with density of macroinvertebrate functional feeding groups as the dependent variable; while the resulting factors of PCA together with fish density, predatory invertebrate's density and deciduous cover were the independent variables. Total density of scrapers, shredders and collectors was used as an independent variable measuring prey availability in predatory invertebrate's regression analysis.

Assumptions of normality of distributions and homogeneity of variances were verified through Shapiro–Wilk and Levene's tests, respectively. Data were $\log_{10}$ and arcsine transformed to fulfil the normality assumption. The significance level for all statistical tests was set at $\alpha = 0.05$. Statistical analyses were performed by means of the STATISTICA 6.1 computer package (StatSoft, Tulsa, Oklahoma, USA).

Results

Environmental factors

There were large differences between streams in concentrations of common ions (Table 1). The PCA revealed 2 main axes accounting for 90.3% of the total variance of physico-chemical water variables between streams (Table 2, Fig. 1). The first factor (PC1-CHEM) was highly positively correlated with temperature and dissolved salts and ions (conductivity, alkalinity, pH, TDS, chloride, sulphate, nitrate, Na^+, K^+, Ca^{2+} and Mg^{2+}). The second factor (PC2-CHEM) reflected the phosphate, nitrite and ammonia levels. Visual inspection of the plots of the first and second components differentiated two groups of streams as to water chemistry. The first factor separated a first group comprising hard water streams (Cabrillas, Gallo and Dulce) with a high mineral content and a second group consisting of soft water streams (Jarama, Cega and Eresma) with low mineral levels (Table 2, Fig. 1). The second axis discriminated between a stream with slight urban and agricultural pollution (Gallo) and non-polluted streams. However, concentrations of phosphate, nitrite and ammonia in the River Gallo were low, since the agricultural activity in the study area is scarce and the population density is low.

Table 1 Mean values (mg L^{-1}, except as noted) of water quality variables for six rivers in central Spain where benthic macroinvertebrates were examined

	Cabrillas	Gallo	Dulce	Jarama	Cega	Eresma
Temperature (°C)	10.2	12.0	13.1	8.6	6.3	6.5
Conductivity (μS cm^{-1})	606.1	963.9	602.4	26.0	17.8	65.3
TDS	303.9	480.9	302.6	13.3	8.9	33.7
pH	7.76	8.07	7.70	7.17	7.14	7.10
Chloride	16.07	85.11	16.73	2.69	0.61	8.65
Sulfate	194.75	126.36	57.01	4.45	2.06	1.97
Phosphate	0.18	0.33	0.13	0.11	0.15	0.10
Alkalinity	281.7	302.6	303.3	11.6	19.2	27.0
Nitrate	7.08	9.92	12.01	0.38	0.94	1.13
Nitrite	0.030	0.107	0.022	0.019	0.036	0.031
Sodium	9.61	52.47	7.76	1.79	1.43	6.85
Potassium	1.82	4.11	1.67	0.71	0.42	0.65
Calcium	128.33	119.54	92.23	2.26	3.27	2.88
Magnesium	27.01	25.43	24.59	0.89	0.78	0.88
Ammonia	0.010	0.100	0.046	0.053	0.029	0.042

Samples were collected from each sampling site every third month from March 1996 to December 1998

Table 2 Factor loadings (unrotated) for the first two principal components (PCs) from principal components analysis of variation in physicochemical variables of 15 sampling localities from 6 rivers in central Spain where benthic macroinvertebrates were studied during 1996–1998

	PC1	PC2
Temperature	**0.877**	−0.155
Conductivity	**0.962**	−0.237
TDS	**0.962**	−0.237
pH	**0.878**	−0.294
Chloride	**0.856**	0.393
Sulfate	**0.942**	−0.205
Phosphate	0.566	**0.753**
Alkalinity	**0.939**	−0.312
Nitrate	**0.862**	0.113
Nitrite	0.558	**0.759**
Sodium	**0.875**	0.075
Potassium	**0.951**	0.291
Calcium	**0.951**	−0.279
Magnesium	**0.949**	−0.298
Ammonia	0.291	**0.888**
Variance explained (%)	72.2	18.1

Loadings in bold were significant ($P < 0.05$)

Habitat variables were significantly different among the study localities (Table 3). The PCA ordination provided a strong discrimination of the localities, with the first two factors accounting for 75.5% of the variance (Table 4). Four variables (altitude, depth, submerged vegetation and substratum) were strongly associated to the first factor (PC1-HAB), while the annual variation in water velocity was related to the second factor (PC2-HAB). The habitat

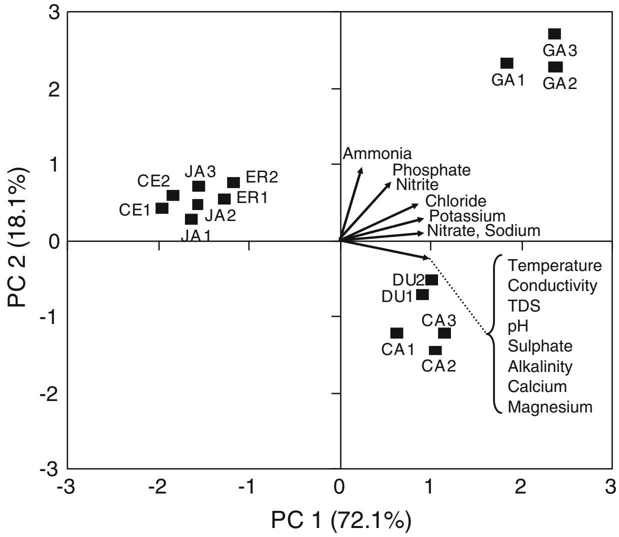

Fig. 1 Plot of the factor scores for physico-chemical variables listed in Table 1 on the first two principal components for 15 sampling localities from 6 Spanish streams in which macroinvertebrate communities were surveyed. *Arrows* show the influence of significant variables in the two axes and *length* indicate their relative importance in determining site distribution. Variance explained (%) by each component is indicated

variables correlated with the first axis described a gradient from localities with greater altitude and coarser substrates at the positive end (rivers Eresma, Cega and headwaters of rivers Jarama and Cabrillas) to streams with greater depth and more submerged vegetation at the negative end (rivers Dulce and Gallo) (Fig. 2). The second axis described a gradient from localities with a higher annual variability in water velocity at the positive end (e.g. Cabrillas3, Jarama2) to localities with an even flow at the negative end (e.g. Gallo2).

Fish communities

Resident brown trout *Salmo trutta* Linnaeus, 1758 is the prevailing fish species throughout the study area. Mean annual estimates of trout density during the study period ranged from 671 fish ha^{-1} in Jarama3 to 5,653 fish ha^{-1} in Eresma1 (Table 3). Other fish species only occurred in Gallo, Dulce and Jarama, where the most abundant were small-sized Cyprinidae, Pyrenean gudgeon *Gobio lozanoi* Doadrio & Madeira, 2004 and Bermejuela *Achondrostoma arcasii* (Steindachner, 1866). Less abundant species were Iberian barbel *Barbus bocagei* Steindachner, 1865, Iberian straight-mouth nase *Pseudochondrostoma polylepis* (Steindachner, 1865), Southern Iberian chub *Squalius pyrenaicus* (Günther, 1868), Gallo chub *Squalius castellanus* Doadrio, Perea & Alonso, 2007 and Calandino *Squalius alburnoides* (Steindachner, 1866). Fish (i.e. macroinvertebrate predators) density varied largely across sampling localities both within and among rivers (Rivers, $F_{5,30} = 13.97$, $P < 0.001$; Localities within rivers, $F_{9,30} = 2.34$, $P < 0.05$; nested ANOVA, Table 3). This

Table 3 Habitat characteristics of 15 sampling localities from 6 rivers in central Spain

	Altitude (m)	Width (m)	Depth (cm)	Velocity (m s^{-1})	Substratum	Submerged vegetation (%)	Canopy (%)	Deciduous cover (%)	Density *S. trutta*	Density Cyprinidae
Cabrillas 1	1,440	2.53	14.61	0.41 (40)	BR, BO (4.62)	0	50.00	150	2,844.7	–
Cabrillas 2	1,280	4.02	18.41	0.53 (33)	BO, CO (3.44)	0	85.70	130	1,257.0	–
Cabrillas 3	1,080	6.29	62.78	0.25 (74)	BR, BO, SI (3.66)	0.62	50.00	170	1,027.1	–
Gallo 1	980	7.68	43.25	0.99 (27)	GR, SI (2.92)	23.11	32.40	60	700.2	574.8
Gallo 2	980	8.21	49.47	0.67 (22)	CO, GR, SI (2.89)	31.74	70.35	115	615.6	707.2
Gallo 3	950	11.16	57.45	0.60 (54)	BO, GR, SI (3.35)	28.06	40.00	120	1,139.0	426.6
Dulce 1	900	4.52	41.85	0.76 (36)	CO, GR, SA (3.14)	10.39	61.59	125	1,780.0	87.2
Dulce 2	870	5.25	50.39	0.40 (51)	GR, SA, SI (2.63)	41.83	38.07	115	950.5	3,146.1
Jarama 1	1,380	3.50	18.80	0.61 (40)	BO, CO (4.36)	0.42	61.34	120	2,324.0	–
Jarama 2	1,160	6.06	31.22	0.45 (66)	BO, CO (4.10)	1.54	48.80	105	1,700.0	29.6
Jarama 3	1,100	8.10	35.73	0.59 (45)	BR, BO, CO (4.20)	1.44	55.42	90	671.2	71.3
Cega 1	1,320	6.01	32.75	0.36 (59)	BO, CO, GR (3.90)	3.00	90.00	40	2,378.0	–
Cega 2	1,180	5.50	24.72	0.54 (50)	BO, CO (4.63)	0	60.00	55	2,605.9	–
Eresma 1	1,340	5.56	22.08	0.54 (48)	BO, CO, GR (4.38)	6.11	67.77	10	5,653.3	–
Eresma 2	1,240	7.08	21.48	0.67 (38)	BO, CO (4.58)	0	63.49	0	4,298.1	–

Mean values were calculated from measurements for each sampling site during the entire study period, 1996–1998. The mean coefficient of variation (%) of water velocity is included in brackets. Substratum index in brackets. Deciduous cover included herb, shrub and tree cover (see "Materials and methods" for details). Mean density (fish ha^{-1}) of fish species in the study localities during 1996–1998 is also shown

BR bedrock, *BO* boulder, *CO* cobble, *GR* gravel, *SA* sand, *SI* silt

Table 4 Factor loadings (unrotated) for the first two principal components (PCs) from principal components analysis of variation in habitat variables of 15 sampling localities from 6 rivers in central Spain where benthic macroinvertebrates were studied during 1996–1998

	PC1	PC2
Altitude	**0.949**	0.035
Width	−0.661	0.309
Depth	**−0.909**	0.295
Velocity	0.055	**0.927**
Canopy	0.522	−0.280
Submerged vegetation	**−0.894**	−0.245
Substratum index	**0.853**	0.369
Variance explained (%)	56.7	18.8

Loadings in bold were significant ($P < 0.05$)

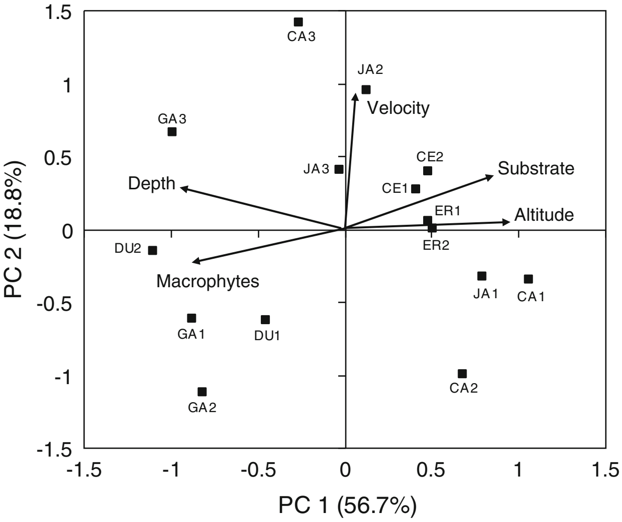

Fig. 2 Plot of the factor scores for habitat variables listed in Table 3 on the first two principal components for 15 sampling localities from 6 Spanish streams in which macroinvertebrate communities were surveyed. *Arrows* show the influence of significant variables in the two axes and *length* indicate their relative importance in determining site distribution. Variance explained (%) by each component is indicated

spatial pattern did not vary among sampling times (sampling time × sampling site interaction, $F_{27,90} = 1.38$, $P > 0.05$).

Benthic communities

The bottom fauna was more abundant in streams draining limestone areas with a higher mineral content (Cabrillas, Gallo, Dulce) compared with those draining rocks of granite with low ionic and carbonate content (Jarama, Cega, Eresma, Table 5). This was particularly evident in Gallo and Dulce, which also have a comparatively more stable discharge and higher temperatures, allowing the occurrence of macrophytes that provide cover for many groups of macroinvertebrates.

The analysis of functional feeding groups showed that predators were the most numerous of taxa (39.6% of total taxa), followed by scrapers (19.8%), shredders (18.8%), collector-gatherers (16.7%), and collector-filterers (5.2%). The most abundant functional feeding group was by far scrapers (mean density 916.8 ind. m^{-2}, 45% of total density; mean biomass 1.03 ind. m^{-2}, 49% of total biomass), followed by collector-filterers (390.0 ind. m^{-2}, 19%; 0.22 ind. m^{-2}, 10%), shredders (344.5 ind. m^{-2}, 17%; 0.46 g m^{-2}, 22%) and collector-gatherers (322.5 ind. m^{-2}, 16%; 0.15 g m^{-2}, 7%); predators only composed a small proportion of the total abundance (62.3 ind. m^{-2}, 3%; 0.24 g m^{-2}, 11%) (Table 5). Mean density and biomass of functional feeding groups varied widely across sampling localities both within (see Table 5) and among rivers (nested ANOVAs, range $F_{5,30} = 3.86–54.57$, $P < 0.001–0.01$), except for predators. This spatial pattern did not vary among sampling times (sampling time x sampling site interaction, range $F_{27,90} = 0.51–1.47$, $P > 0.05$).

The first two axes of the CA ordination accounted for most of the variation in the macroinvertebrate abundance data, with eigenvalues of 0.20 and 0.18 for axis 1 and 2, respectively. The total inertia (total variation in the data) was 0.49 and the first two axes explained 76.9% of this variation (Fig. 3). Correspondence analysis showed that functional group attributes were somewhat different between localities. The second axis of the CA separated the sampling localities of River Gallo. This stream with the higher abundances of scrapers and filtering collectors appear clearly segregated to the others. The first axis gathers soft water streams with little abundances to hard water streams with high densities and dominated by shredders and scrapers. A majority of localities (Cabrillas1, Cabrillas2; rivers Jarama, Cega and Eresma) were dominated by gathering collectors (mean 39.4%), mainly Ephemeroptera *Baetis* sp. and Diptera Chironomidae. Scrapers were also important in Jarama1 and Eresma1 (mean 30.4%), with Ephemeroptera (e.g. *Rithrogena* sp.) and Coleoptera (*Normandia* sp.) as the dominant taxa. Likewise, Dulce1, Gallo2 and Gallo3 were mainly dominated by scrapers (mean 60.5%) due to the high number of the Coleoptera *Elmis* sp. and the molluscan *Potamopyrgus antipodarum* (Gray, 1843). Localities Cabrillas3 and Dulce2 were dominated by shredders (mean 45%) due to the high number of the crustacean *Echinogammarus berilloni* (Catta, 1878). Gallo1 was dominated by filtering collectors (mean 50%) because of the high density of Simuliidae. Finally, predators were a scarce group in all localities (mean 5.9%) and were dominated by the anisopteran *Onycogomphus uncatus* (Charpentier, 1840).

Table 5 Mean density (ind. m^{-2}) and biomass (g m^{-2}, in brackets) of invertebrate functional feeding groups (GCOL, FCOL, SHR, SCR, PRE) in the study localities during 1996–1998

	GCOL	FCOL	SHR	SCR	PRE
Cabrillas 1	957.6 (0.43)	450.8 (0.52)	173.7 (0.23)	336.8 (0.30)	122.0 (0.30)
Cabrillas 2	454.9 (0.20)	228.1 (0.38)	97.8 (0.13)	176.7 (0.16)	35.7 (0.10)
Cabrillas 3	175.8 (0.06)	223.3 (0.16)	855.8 (1.01)	940.9 (0.71)	60.9 (0.49)
Gallo 1	365.9 (0.20)	2971.4 (1.00)	517.9 (0.56)	1998.2 (2.24)	51.0 (0.50)
Gallo 2	639.9 (0.27)	1038.7 (0.34)	597.4 (0.82)	3126.9 (3.59)	76.7 (0.25)
Gallo 3	491.9 (0.23)	175.6 (0.10)	749.3 (0.98)	5031.1 (7.01)	78.4 (0.42)
Dulce 1	231.9 (0.16)	218.7 (0.22)	425.1 (0.45)	896.2 (0.69)	100.6 (0.19)
Dulce 2	213.4 (0.23)	160.6 (0.25)	1,254.7 (2.55)	659.8 (0.60)	90.8 (0.27)
Jarama 1	105.2 (0.04)	90.3 (0.06)	65.2 (0.05)	175.7 (0.11)	48.3 (0.20)
Jarama 2	149.0 (0.16)	14.7 (0.06)	31.3 (0.06)	164.8 (0.10)	45.0 (0.09)
Jarama 3	201.0 (0.04)	31.6 (0.08)	25.7 (0.02)	148.1 (0.06)	54.4 (0.35)
Cega 1	238.0 (0.11)	48.5 (0.05)	142.5 (0.04)	128.1 (0.07)	55.6 (0.34)
Cega 2	409.8 (0.15)	56.0 (0.06)	236.7 (0.09)	207.4 (0.10)	89.6 (0.11)
Eresma 1	204.1 (0.06)	137.7 (0.09)	80.4 (0.05)	233.7 (0.11)	48.1 (0.22)
Eresma 2	267.3 (0.06)	145.3 (0.04)	25.7 (0.01)	99.1 (0.08)	41.6 (0.15)
Density	$F_{9,30} = 4.13$, $P < 0.01$	$F_{9,30} = 2.31$, $P < 0.05$	$F_{9,30} = 6.63$, $P < 0.001$	$F_{9,30} = 5.55$, $P < 0.001$	$F_{9,30} = 1.34$, $P > 0.05$
Biomass	$F_{9,30} = 3.95$, $P < 0.01$	$F_{9,30} = 3.02$, $P < 0.01$	$F_{9,30} = 6.89$, $P < 0.001$	$F_{9,30} = 9.43$, $P < 0.001$	$F_{9,30} = 1.41$, $P > 0.05$

Results of nested ANOVA analyses for differences in density and biomass across sampling localities within rivers are also shown

GCOL gathering collectors, *FCOL* filtering collectors, *SHR* shredders, *SCR* scrapers, *PRE* predators)

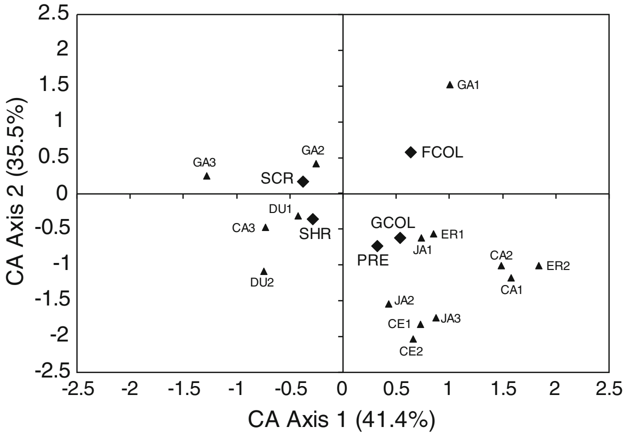

Fig. 3 Correspondence analysis (CA) ordination of the macroinvertebrate density data collected during the period 1996–1998 in 15 sampling localities from 6 Spanish rivers (*GCOL* gathering collectors, *FCOL* filtering collectors, *SHR* shredders, *SCR* scrapers, *PRE* predators)

Relationship between environmental factors, fish and benthic communities

Multiple regression analyses revealed a significant relationship between density and biomass of gathering and filtering collectors, and chemical features related to water mineralisation and temperature (PC1-CHEM), which accounted for 57 and 43% (GCOL) and 76 and 50% (FCOL) of the variance explained by the models, respectively (Table 6). Ionic and nutrient content of water (PC1-CHEM and PC2-CHEM) and the habitat characteristics (PC1-HAB) were the variables with the greatest effect on shredder density and biomass, accounting for 59 and 85% of the variation, respectively. Thus, abundance of shredders was higher in deeper localities with macrophytes and higher nutrient and ionic content (Table 6). Density and biomass of scrapers was related to the water concentration of salts and ions as well as to the habitat in the case of density, which accounted for the 90 and 74% of the variance, respectively. Density of scrapers was also higher in deeper localities at lower altitudes and with abundant macrophytes. Finally, density and biomass of macroinvertebrate predators was related, respectively, to prey density and biomass, accounting for 34 and 50% of the variance. Therefore, density and biomass of major functional feeding groups tended to be higher in hard waters and warmer localities, despite fish predator abundance and allochthonous food availability (deciduous cover).

Discussion

The functional organization of the macroinvertebrate communities in most study reaches did not correspond with that predicted for undisturbed forested headwater streams by Vannote et al. (1980). Hence, the frequencies did not follow the hypothetical co-dominance of collectors with

Table 6 Results of stepwise multiple regression analyses testing the effect of four principal components (PC1-CHEM, PC2-CHEM, PC1-HAB, PC2-HAB), cover of deciduous riparian vegetation, and abundance of benthic and fish predators, on density and biomass of macroinvertebrate functional feeding groups in 15 sampling localities from 6 rivers in central Spain during 1996–1998

Model	Dependent variable	Independent variables	Coefficient	SE	*P*
$r^2 = 0.566$, $F = 7.83$	Density GCOL	PC1-CHEM	0.239	0.061	<0.01
		Constant	2.428	0.047	<0.001
$r^2 = 0.432$, $F = 9.88$	Biomass GCOL	PC1-CHEM	0.025	0.008	<0.01
		Constant	0.060	0.008	<0.001
$r^2 = 0.756$, $F = 18.61$	Density FCOL	PC1-CHEM	0.405	0.089	<0.001
		Constant	2.158	0.084	<0.001
$r^2 = 0.497$, $F = 12.83$	Biomass FCOL	PC1-CHEM	0.054	0.015	<0.01
		Constant	0.077	0.015	<0.001
$r^2 = 0.593$, $F = 18.95$	Density SHR	PC1-CHEM	0.427	0.098	<0.001
		Constant	2.224	0.099	<0.001
$r^2 = 0.848$, $F = 20.48$	Biomass SHR	PC1-HAB	−0.138	0.022	<0.001
		PC2-CHEM	0.085	0.025	<0.01
		Constant	−0.024	0.087	>0.05
$r^2 = 0.895$, $F = 51.28$	Density SCR	PC1-CHEM	0.352	0.067	<0.001
		PC1-HAB	−0.228	0.070	<0.01
		Constant	2.573	0.052	<0.001
$r^2 = 0.898$, $F = 52.65$	Biomass SCR	PC1-CHEM	0.140	0.049	<0.05
		Constant	0.201	0.038	<0.001
$r^2 = 0.343$, $F = 6.80$	Density PRE	Density prey	0.059	0.022	<0.05
		Constant	1.216	0.215	<0.001
$r^2 = 0.501$, $F = 13.08$	Biomass PRE	Biomass prey	0.074	0.021	<0.01
		Constant	0.056	0.013	<0.001

The models for benthic predators also included the density and biomass of benthic prey as independent variables

PC1-CHEM, salts and ions; *PC2-CHEM*, nutrients; *PC1-HAB*, habitat characteristics; *PC2-HAB*, water velocity variation

GCOL gathering collectors, *FCOL* filtering collectors, *SHR* shredders, *SCR* scrapers, *PRE* predators)

shredders. On the contrary, scrapers were a major group, especially in Dulce and Gallo where the invasive mud-snail *P. antipodarum* mostly contributed to benthos abundance. However, when this species was removed from the analyses, invertebrate communities were dominated mainly by shredders and gatherers, as reported previously in other undisturbed canopied upper reaches (e.g. Hawkins and Sedell 1981; Friberg 1997; Maridet et al. 1998).

The abundance of major functional groups was positively related to the water concentration of salts and ions. Shredder biomass and scraper density were also influenced by habitat characteristics, the abundance increasing in lower deeper localities with abundant macrophytes, which corresponded to hard water basins Dulce and Gallo. Maybe shredders were more abundant in these habitats where coarse-particulate organic matter (CPOM) could accumulate. These lower stream sections support greater abundances of scrapers probably because increasing light enhances periphyton growth. Finally, the abundance of predatory invertebrates was to some extent controlled through the density and biomass of benthic prey.

Our results corroborate previous evidence on the influence of water chemistry on macroinvertebrate abundance in rivers (e.g. Peterson et al. 1993; Buss et al. 2002; Benstead et al. 2005). The importance of water chemistry in governing zoobenthos is well documented. Aquatic chemistry variables are frequently used to explain the variation in macroinvertebrate communities in lentic systems (Heino 2000; Free et al. 2009). Alkalinity has been shown to be significant in determining the littoral community composition of lakes close to reference condition in Europe (Little et al. 2006) and also as a significant covariate affecting the response of many ecological assessment metrics when tested alongside variables indicative of eutrophication such as total phosphorus and chlorophyll *a* (O'Toole et al. 2008).

Further, theoretical and empirical work in detritus-based systems show that both primary and secondary consumers respond positively to increased resource availability (e.g. Gulis and Suberkropp 2003; Cross et al. 2006). For example, nutrient addition to streams has resulted in increased detrital quality, measured as increased microbial biomass and activity. Cross et al. (2006) work provided evidence that nutrient enrichment in detritus-based systems can stimulate whole-community production through detrital–microbial pathways.

Density of shredders and gatherers was expected to be related to the cover of deciduous vegetation, as a surrogate measure of detritus resource. In forested streams, the supply of detritus play a major role in trophic dynamics, also providing refuge for many invertebrates (e.g. Wallace et al. 1997; Hall et al. 2000; McIntosh et al. 2005). Changes in coarse (CPOM) and fine particulate organic matter (FPOM) are attributed to changes in riparian vegetation (Shieh et al. 2003; Danger and Robson 2004). Shredding invertebrates transform CPOM to FPOM thus contributing to the primary input of nutrients into the food web (Merritt and Cummins 1996). Nutrient concentrations may also influence the breakdown of leaf litter (Paul and Meyer 2001; Spanhoff et al. 2007). However, litter retention or breakdown may be different between streams, which is likely given the differences in flow regime and physical variables (Prochazka et al. 1991; Hoover et al. 2006). Therefore, riparian condition may not correspond to instream detritus resources.

Our findings contrast with most studies that examined the simultaneous effect of predators and detrital food resources on macroinvertebrate communities. In New Zealand grassland streams, Flecker and Townsend (1994), McIntosh and Townsend (1996) and Huryn (1998) found a differential effect of predatory fish on benthic macroinvertebrates. These authors showed experimentally that exotic brown trout exerted a strong control on primary consumers, whereas predation by native river galaxias *Galaxias eldoni* McDowall and predatory invertebrates had a weak effect. They concluded that ecosystem productivity was controlled by predation regime, through a trophic cascade process. However, brown trout in New Zealand rivers is an exotic species showing densities much greater (mean 7,000 fish ha^{-1}) than those of the present study (see Table 3). Nyström et al. (2003) in upland New Zealand streams found that predatory brown trout (mean 4,700 fish ha^{-1}) and variations in resource supply associated with the presence of a forest canopy had significant but largely independent effects on the invertebrate community structure. Further, McIntosh et al. (2005) provided evidence for the influence of both brown trout predation and leaf pack biomass in populations of a stream detritivore on a detritus-based stream food web. These results support a role for both habitat effects and fish predation in regulating the structure of macroinvertebrate communities, albeit in disturbed ecosystems by the introduction of the predatory brown trout.

In contrast with previous research, a control of invertebrate communities by fish predation was not observed in the study streams. Although invertebrate predators may have stronger effects on benthic prey than predatory fish (Wooster 1994; Englund et al. 1999), this was not the case in our study. Our findings agree with those of Rosemond et al. (2001) in Costa Rica rivers, where detritus-based food webs were experimentally enriched with phosphorous. These authors found that positive effects of nutrients on insect biomass were greater than negative effects of macroconsumers (fish and shrimps). The majority of previous studies on the role of predators in influencing prey population dynamics in detrital-based stream food webs have been based on the presence/absence of fish, not including the variability of fish density among sites. The present study considered interannual variations in both invertebrates and fish abundances over a wide range of environmental conditions, a spatio-temporal scale large enough to assess the influence of habitat and predation.

Previous studies analysing the effects of fish predation on macroinvertebrate communities show that drift-feeding salmonids have few or no effects on benthic prey, but benthic-feeding fishes (cyprinids, cottids) significantly reduce prey populations (e.g. Cooper et al. 1990). Most Iberian fish species are insectivorous while omnivory is not a common feeding strategy (Ribeiro et al. 2008). However, in our streams densities of cyprinids are probably not high enough to exert a significant effect on macroinvertebrate communities. Further, factors such as prey vulnerability and quality of alternative food sources for brown trout may influence the relative strength of predator control. Several studies indicate that visually hunting fish such as brown trout are selective consumers that prefer large active prey (e.g. predatory invertebrates and large shredders), and feed less on small prey or prey protected by cases or shells (Dahl 1998; De Crespin de Billy and Usseglio-Polatera 2002). Inputs of terrestrial invertebrates derived from surrounding forest may also reduce the impact of drift-feeding fish on the abundance of benthic prey (e.g. Dahl and Greenberg 1996; Nakano et al. 1999; Kawaguchi and Nakano 2001). Moreover, the effects of fish on invertebrates should be strongest in streams with high densities of fish and low densities of invertebrates (Reice 1991). In the study streams fish species are currently exploited by angling (Nicola et al. 2009) and probably populations do not reach densities high enough to control benthic communities.

Our findings lend support to Rosenfeld's (2000) hypothesis that detritivores in detritus-based food chains appear to be primarily influenced by bottom-up forces, while grazers in algal-based food chains are more strongly influenced by top-down effects. The finding that benthic macroinvertebrate communities in undisturbed headwater streams are mainly affected by water chemistry variables irrespective of fish predation and habitat features clearly highlight the sensitivity of functional feeding groups to changes in chemical features and their role as indicators for bioassessment. Our analyses also add to the pattern formerly observed for fish production in headwater streams, which was limited by water chemical features related to dissolved salts and ions, thus pointing out the relevant role of water chemistry in these food webs (Almodóvar et al. 2006).

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